Warming shortens flowering seasons of tundra plant communities

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Authors: Janet S. Prevéy[*1,2], Christian Rixen[2], Nadja Rüger[3,4], Toke T. Høye[5], Anne D. Bjorkman[6,7], Isla H. Myers-Smith[8], Sarah C. Elmendorf[9,10], Isabel W. Ashton[11], Nicoletta Cannone[12], Chelsea Chisholm[13,2], Elisabeth J. Cooper[14], Bo Elberling[15], Anna Maria Fosaa[16], Greg H.R. Henry[17], Robert D. Hollister[18], Ingibjörg Svala Jónsdóttir[19], Kari Klanderud[20], Christopher W. Kopp[21], Esther Lévesque[22], Marguerite Mauritz[23], Ulf Molau[24], Susan Natali[25], Steve Oberbauer[26], Zoe A. Panchen[27], Eric Post[28], Sabine B. Rumpf[29], Niels Martin Schmidt[5], Edward Schuur[30], Philipp R. Semenchuk[29,14], Jane G. Smith[31], Katharine N. Suding[10,31], Ørjan Totland[32], Tiffany Troxler[26], Susanna Venn[33], Carl-Henrik Wahren[34], Jeffrey M. Welker[35,36], Sonja Wipf[2]

Author affiliations:

1. Pacific Northwest Research Station, USDA-Forest Service, 3625 93rd Avenue SW, Olympia, Washington 98512
2. WSL Institute for Snow and Avalanche Research SLF, 7260 Davos, Switzerland
3. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
4. Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama
5. Department of Bioscience and Arctic Research Centre, Aarhus University, Denmark
6. Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Denmark
7. Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany
8. University of Edinburgh, Scotland
9. National Ecological Observatory Network, 1685 38th Street, Suite 100, Boulder, Colorado 80301, USA.
10. Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado 80309, USA.
11. Northern Great Plains Inventory and Monitoring Network, National Park Service, Rapid City, SD, USA
12. Department of Science and High Technology, Università degli Studi dell'Insubria, Como, Italy
13. Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Universitetsparken 15, DK-2100 Copenhagen
14. Institute for Arctic and Marine Biology, The Arctic University of Norway, N-9037 Tromsø, Norway
15. Center for Permafrost (CENPERM), Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark
16. Faroese Museum of Natural History, Faroe Islands
17. Department of Geography, University of British Columbia, Vancouver, BC, Canada
18. Biology Department, Grand Valley State University, 1 Campus Drive, Allendale, MI 49401, USA
19. School of Engineering and Natural Sciences, University of Iceland, Iceland
20. Department of Ecology and Natural Resources, Norwegian University of Life Sciences, Norway
21. Department of Botany, University of British Columbia, Vancouver, BC, Canada

22. Université du Québec à Trois-Rivières, Québec, Canada
23. Center for Ecosystem Science and Society Center, Northern Arizona University, Flagstaff, AZ, USA
24. Department of Biology and Environmental Sciences, University of Gothenburg, Sweden
25. Woods Hole Research Center, Falmouth, MA, USA
26. Department of Biological Sciences, Florida International University, FL, USA
27. Department of Biology, Dalhousie University, Canada
28. Department of Wildlife, Fish, & Conservation Biology, University of California, Davis
29. Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria
30. Center for Ecosystem Science and Society Center, Northern Arizona University, Flagstaff, AZ, USA
31. Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO, USA
32. Department of Biology, University of Bergen, Bergen, Norway
33. Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Victoria, Australia 3125
34. Research Centre for Applied Alpine Ecology, La Trobe University, Bundoora 3086, Australia
35. UArctic and University of Oulu, Finland
36. Department of Biological Sciences, University of Alaska Anchorage, AK, USA

Corresponding author details: Janet Prevéy, +1 360-701-6466, jprevey@fs.fed.us

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Abstract

Advancing phenology is one of the most visible effects of climate change on plant communities, and has been especially pronounced in temperature-limited tundra ecosystems. However, phenological responses have been shown to differ greatly between species, with some species shifting phenology more than others. We analyzed a database of 42,689 tundra plant phenological observations to show that warmer temperatures are leading to a contraction of community-level flowering seasons in tundra ecosystems due to a greater advancement in flowering times of late-flowering species than of early-flowering species. Shorter flowering seasons with a changing climate have the potential to alter trophic interactions in tundra ecosystems. Interestingly, these findings differ from those of warmer ecosystems, where early flowering species have been found to be more sensitive to temperature change, suggesting that community-level phenological responses to warming can vary greatly between biomes.

Main

Warmer temperatures associated with climate change have advanced the phenology of organisms around the world [1–3], and both temperature increases and phenological changes have been especially pronounced in temperature-limited tundra ecosystems [4–7]. Tundra ecosystems encompass cold regions above latitudinal treeline (Arctic tundra) or altitudinal treeline (alpine tundra). Remote sensing studies indicate broad patterns of changing seasonality of vegetation productivity at high latitudes over time in relation to climate warming [8–10], however, phenological responses to warmer temperatures have been shown to differ greatly among species and locations, with some species shifting dates of flowering and flower senescence more than others [11–15]. Studies from temperate ecosystems have found that early-flowering species often advance phenological events more in response to warmer temperatures than later-flowering species [16,1,17–19], however, to date, the relationship between

flowering time and phenological sensitivity has not been tested across high-altitude tundra ecosystems.

Evidence suggests that across northern tundra ecosystems, phenology of plants from colder sites at higher latitudes changes more with warmer temperatures than phenology of plants from warmer, more southern latitudes [7,15,20]. However, within tundra plant communities, phenological responses to warming are often species-specific, with no clear responses of specific functional groups [21–27,3] or phylogenetic relationships [28]. A better understanding of the drivers of variation in phenological sensitivity will help determine how species and plant communities will respond to climate change in the future [23,29,3], as well as contribute to our understanding of the adaptive nature of species-specific phenological responses to climate change.

The timing of life history events, such as flowering, is of critical importance in harsh tundra ecosystems, and the fitness consequences of different phenological responses to climatic drivers can be substantial [30,31]. Plants that track snowmelt dates and not temperature (or thermal sums) may risk exposure to freezing events that can damage flowers and reduce seed production during early snowmelt years [32–35], whereas plants that flower too late risk not being able to fully develop seeds before the end of the growing season, and may be at a competitive disadvantage to plants that do respond [22,36].

There are a diversity of life history strategies among species in tundra plant communities, even within the short growing seasons experienced at high latitudes and altitudes [21,22,37]. These various strategies could influence the species-specific responses of plants to warmer temperatures [37,38,12]. The relative flowering time of a species compared to other species in the plant community (hereafter its "phenological niche") could help explain the variation in phenological responses among species in tundra ecosystems. The existence of different phenological niches could promote species coexistence in many ecosystems [39–41], as phenological niches can strongly influence competitive and trophic interactions [42]. Differential

134 shifts in the phenological niche could lead to trophic mismatches in tundra ecosystems,
135 altering food webs and influencing the abundance of pollinators or herbivores [43–45,12].
136 Classifying organisms using phenological niches could thus be a useful way to predict how
137 species will respond to changes in environmental conditions in the future [38].

138 Measuring the relative importance of different environmental cues for Arctic and
139 alpine species, such as temperature and snowmelt date, will help determine how species will
140 respond as the climate warms [23,29]. Although temperature influences the date of snowmelt,
141 snowmelt can be decoupled from temperature because snowmelt is also influenced by the
142 amount and quality of precipitation over winter and spring [13]. The phenology of early-
143 flowering plant species may be influenced more by photoperiod or the timing of snowmelt,
144 whereas the phenology of late-flowering species is probably more dependent on thermal heat
145 sums accumulated over the growing season [22,46]. If early-flowering tundra species are less
146 responsive to changes in summer temperature than late-flowering ones, then increases in
147 summer temperature will likely accelerate the flowering phenology of late-flowering species
148 more than early-flowering ones. Additionally, if temperatures towards the end of the growing
149 season are rising more rapidly than temperatures at the beginning of the year, then flowering
150 phenology of late-flowering species will advance more than that of early-flowering species
151 [14,15]. In both cases, a more rapid advance of late- than early-flowering species would result in
152 a contraction of the community-level flowering season (Fig. 1, [12], which could substantially
153 change competitive and trophic interactions [47,44,12,31]. In particular, shorter flowering seasons
154 could also strongly limit resource availability for pollinators, especially if the phenology of
155 pollinator species are responding to different drivers than plant communities [12,48].

156 In this data synthesis, we test how the temperature sensitivity of flowering relates to
157 the phenological niches of tundra species using flowering observations of a total of 253
158 species, 23 sites, and up to 20 years from Arctic and alpine ecosystems around the world, both
159 from long-term monitoring plots and warming experiments (Fig. 2). With this global dataset,

we tested three main hypotheses: **1)** flowering phenology of late-flowering tundra species is more sensitive to warmer summer temperatures than flowering phenology of early-flowering species. We tested this hypothesis with both observational and experimental data, and hypothesized that: **1a)** results would be similar for both observational and experimental data; that is, late-flowering species would be more sensitive to natural *and* experimental warming. **2)** If late-flowering species are flowering earlier, but early-flowering species are not, then the community-level flowering seasons will be shorter in warmer years, and thus, **3)** as average summer temperatures at tundra sites have warmed in the recent past, the duration of community-level flowering seasons have decreased over this time period. We examined how the phenological niche of a species influenced the sensitivity of first flowering dates (FFDs) and flower senescence dates (LFDs) to summer temperature indices, snowmelt date, and experimental warming. To test for a contraction of community-level flowering seasons with warmer summers and over time, we compared the community flowering season length to mean June-July temperatures and year for six sites with observations of four or more species over 10 or more years.

Results

First flowering dates (FFDs) of late-flowering species were more temperature sensitive than early-flowering species (i.e., FFDs of late-flowering species advanced more per ºC increase in summer temperature, and in response to experimental warming, than early-flowering species, Figs. 3A and 4A, Supplementary Fig. 1, Supplementary Table 4). Results of analyses using June temperature for all species, or the average daily temperature from snowmelt through the average flowering date, also indicated a significant influence of phenological niche on temperature sensitivity of flowering (Figs. 3B and 3C, Supplementary Table 4). However, the phenological niche of a species did not influence the sensitivity of FFDs to snowmelt timing (Fig. 3D, Supplementary Table 4). Overall, species from sites with

colder summer temperatures had greater temperature sensitivity of FFDs (Supplementary Table 4). Analyses from warming experiments yielded similar results, with greater differences in FFDs between experimentally warmed and control plots for late-flowering species than for early-flowering species (Fig. 4A). There was no influence of phenological niche on the temperature sensitivity of flower senescence dates (LFDs) in either long-term monitoring plots or warming experiments (Supplementary Table 5 and Fig. 4B).

The community-level flowering seasons across the six sites with 10 or more years of data were 3.96 days shorter per 1 °C warmer June-July temperature (95% CI = -7.31, -0.79, Fig. 5A, Supplementary Table 5). The length of the flowering season was estimated as the duration between the average FFD of the earliest and average LFD of the latest flowering species per site in each year. Community-level flowering seasons became shorter over time in all six sites, but the change was significant only at Alexandra Fiord, Daring, and Zackenberg. Across all sites, flowering season length shortened by 0.43 days per year, but the credible interval on this parameter overlapped zero (95% CIs = -0.87, 0.06, Fig. 5B). Annual June-July temperatures

Discussion

Our results reveal an overall shortening of community-level flowering seasons with summer warming across the tundra biome. We additionally found evidence of a contraction of the community-level flowering season over time at a subset of sites. In both cases, the shortening of the flowering season was due to greater temperature sensitivity of flowering of late-flowering than early-flowering species. On average, the temperature sensitivity of first flowering dates was greater for tundra species that flowered later in the growing season compared to those that flowered earlier. This pattern was evident both in long-term monitoring plots over time and in warming experiments. Additionally, observations from long-term monitoring plots indicated that, on average, plants at colder sites were more

212 phenologically sensitive, consistent with results from Prevéy et al. (2018) using a largely
213 overlapping dataset, and that late-flowering plant species at the coldest tundra sites exhibited
214 the highest phenological sensitivities in the dataset. Our analyses of long-term monitoring and
215 experimental warming data indicate that late-flowering tundra species may alter their
216 flowering phenology more than early-flowering ones in a warmer world, resulting in a
217 shortening of community-level flowering seasons at sites across the tundra biome.

218 The finding of greater temperature sensitivity of late-flowering species differs from
219 results of many studies conducted at lower latitudes and altitudes[6,49,18,19]. Studies from warmer
220 biomes found that early-flowering species often advance phenological events more in
221 response to warmer temperatures than late-flowering species [16,1,17–19,50,51]. Mid- and late-
222 season moisture limitation probably plays a greater role in structuring the phenology of plants
223 in warmer ecosystems [52]. However, in cold tundra ecosystems with relatively short summers,
224 moisture limitation may not be as important a phenological driver as in warmer, drier
225 ecosystems [53]. Additionally, selection might be stronger at the start of the growing season
226 under the harsher climate conditions experienced by early flowering plants in tundra sites
227 relative to more temperature biomes [46].

228 Our finding of a contraction of the flowering season with warmer temperatures also
229 differs from studies in other ecosystems. Some studies have found a divergence of flowering
230 dates of early- versus late-flowering species with warming in temperate grasslands [49],
231 montane and subalpine meadows [54,55], and deserts [53], with less overlap in the flowering times
232 of species [49], and a mid-season depression in flower abundance [54,55]. Individual studies
233 conducted in temperate ecosystems and global meta-analyses of phenology experiments and
234 long-term monitoring projects have concluded that early-flowering species are more
235 responsive to climate warming [18,6,51]. However, our results show that Arctic and alpine plants
236 exhibit the opposite pattern, suggesting that community-level phenological responses to
237 warming can vary greatly among biomes [19,56].

For the six Arctic sites with over ten years of observations, we documented a contraction of the flowering season with warmer temperatures, and a trend toward shorter flowering seasons over time, although this pattern was not significant at all sites. A contraction of the flowering season is in agreement with previous single-site studies in arctic ecosystems [5,12,48]. Shorter flowering seasons could lead to possible phenological mismatches if late-season pollinators or herbivores are not following the same cues as late-season plant species [48,57]. Additionally, less dispersion among the flowering times of species in a community may increase competition for pollinators [58] or, alternatively, increase exposure to more pollinators because plant species are all flowering at similar times [59]. However, it is important to note that we did not directly measure how the abundance of plant species, or the abundance of open flowers, changed with temperature or over time. The timing of peak flowering may shift less than the timing of first flowering dates[55], thus changes in coverage and abundance of flowers over the season may exhibit different patterns than changes in the overall length of the flowering season[60].

Increased temperature sensitivity of flowering may be advantageous if it allows plants to track ideal temperature conditions for growth and reproduction [61,30]. Our results suggest that late-flowering species that track temperature more than snowmelt date or photoperiod may be more able to optimize the timing of flowering and could have an advantage as temperature increases or becomes more variable [62]. Phenological plasticity may also be indicative of plasticity of other plant traits, so plant species that can shift phenology to changing conditions may be better able to adjust to climate change over time. To date, there have been few studies comparing phenological traits to other plant traits and changes in plant abundance (but see 30, 61). However, as the amount of phenological data available for tundra plant species accumulates, the next logical step will be linking phenological measurements to performance measurements to aid predictions of vegetation change in tundra ecosystems in the future [64].

Phenological responses are one of the most easily observable effects of climate change on plant communities [2], but identifying the underlying mechanisms driving phenological responses to warming is crucial to accurately estimating food-web dynamics and plant-pollinator interactions. Our data synthesis demonstrates an agreement between long-term and experimental data to identify how plants respond to warmer temperatures [65,66]. In temperature-limited tundra ecosystems, late-flowering species advance flowering more in warmer years, and this can lead to a contraction of the flowering season of the entire plant community. Additionally, these changes are most pronounced at the coldest tundra sites where temperature increases have been greatest [20]. Thus, our study demonstrates that the phenological niches of plant species can be useful predictors of how the flowering of tundra species will respond to warmer temperatures, and can aid predictions of plant and ecosystem responses to climate change in the future.

Methods

Compilation of the flowering phenology database

We compiled a database of flowering phenology observations from a total of 253 species at 23 sites in Arctic and alpine ecosystems from both long-term monitoring plots and warming experiments (Supplementary Table 1, Fig. 2). Portions of the dataset were analyzed and reported in Oberbauer et al. (2013) and Prevéy et al. (2017), however, two additional monitoring sites and 10 additional warming experiments are included in this analysis (Supplementary Table 1). Each site collected phenological observations following a standardized protocol that was originally developed for the International Tundra Experiment (ITEX) network [67,68]. Following the ITEX protocol, observers recorded the phenological status of plants one to three times per week over the snow-free season, and specifically recorded the first flowering date (FFD) and last flowering date (LFD) of each species per individual or plot. The FFD was defined as the date when the first flower was open, the first

290 pollen was visible, or the first anthers were exposed. The LFD was defined as the date when
291 the withering of anthers, first petal drop, or last petal drop was observed. However, both FFD
292 and LFD were recorded consistently at each site over time. We include data only from long-
293 term monitoring plots that had three or more years of flowering phenology observations per
294 species per plot.
295
296 ***Effects of species phenological niches on the sensitivity of flowering***
297 We calculated the phenological niche of a species at each site as the average first
298 flowering date of the species at each site across all years of measurements [50] (Supplementary
299 Table 2). We examined the relationship between phenological niche and temperature
300 (expressed in several ways) and snowmelt dates at long-term monitoring plots. Temperature
301 was expressed as the mean monthly temperature until flowering, mean June temperature, or
302 the mean daily temperature between snowmelt and flowering. Flowering dates for the
303 Southern hemisphere alpine site were adjusted by 210 days to match that of the Northern
304 hemisphere growing season, and to assist with model convergence in analyses. We specified
305 mean monthly temperature until flowering separately for each species and site as the average
306 monthly air-temperature from June through the average month of flowering, except for 29 site
307 by species combinations where species flowered in May, for which we used average May
308 temperature (Supplementary Table 2). For example, if the phenological niche of a species was
309 June 30th, then mean June temperature was used as the summer temperature variable for that
310 species. However, if the phenological niche was July 15th, then average June-July temperature
311 was used (Supplementary Table 2). To test the influence of the temperature windows on the
312 results we obtained, we also performed the analyses with June temperature as the predictor
313 variable for all sites and species, because preliminary analysis showed that June temperature
314 was the strongest predictor of flowering across all species and sites (Supplementary Table 2).
315 We used average monthly temperatures because they were available for all sites in the

316 analyses; thus allowing us to incorporate the largest set of phenological data available. We
317 recognize that using monthly mean temperatures may bias results, as sensitivity of flowering
318 time for species flowering in the early parts of months are obviously not affected by
319 temperatures experienced after they flower. Thus, for the subset of 12 sites with both daily
320 temperature data and snowmelt dates available we calculated the mean daily temperature
321 between snowmelt and flowering as the average daily air temperature from the date of
322 snowmelt through the average date of flowering for each species and year. Finally, we
323 examined the association between the timing of snowmelt and flowering in long-term
324 monitoring plots by comparing the phenological niches of species to snowmelt timing for the
325 subset of 13 sites that had recorded snowmelt dates over time.

326 Models also included the effect of mean site-level summer temperatures (June-Aug)
327 from 1981-2000 as an additional predictor variable of species phenological responses, since a
328 previous synthesis found that flowering dates of species from colder tundra sites were more
329 sensitive to changes in temperature than those from warmer sites [20]. Mean monthly
330 temperatures for sites were obtained from local weather stations when available. If no long-
331 term (1981–2010) weather data were available near sites, then mean monthly temperatures
332 were estimated using 0.5° gridded temperature data from the Climate Research Unit (CRU)[69]
333 (Supplementary Table 1). Temperatures and phenological niches were mean-centered by site
334 for all species for long-term monitoring plot data. Plot within site, and year within site, were
335 included as random variables. We also tested for the interaction between phenological niche
336 and temperature.

337 In total, the analyses of FFDs with summer temperature windows or mean June
338 temperatures as predictor variables included 14,324 observations from 318 unique site by
339 species combinations at 19 sites. The analyses of FFDs with snowmelt date included 9,918
340 observations from 141 unique site by species combinations at 13 sites, and the analyses of
341 FFDs using average daily temperatures included 9,713 observations from 143 unique site by

species combinations at 11 sites. The analyses of LFDs with summer temperature windows or mean June temperatures as predictor variables included 9,226 observations from 88 unique site by species combinations at 11 sites. The analyses of LFDs with snowmelt date included 7,661 observations from 80 unique site by species combinations at 11 sites, and the analyses of LFDs using average daily temperatures included 7,341 observations from 74 unique site by species combinations at 9 sites.

Effects of phenological niches on the temperature sensitivity of flowering in warming experiments

We examined observations from warming experiments that utilized open-top chambers (OTCs) to investigate how experimental warming influenced the flowering dates of species with different phenological niches. In the warming experiments, plots were warmed with ca. 1 m^2 fiberglass or polycarbonate OTCs, in either cone or hexagonal shapes, that increased air temperature by 0.5-3 ºC [67,70–72], Supplementary Table 3). The OTCs were placed on plots either only over the summer, or left on plots year-round, depending on the site (Supplementary Table S3).

To examine how the phenological niche of a species influenced its phenological sensitivity to experimental warming, we first calculated the average difference in the timing of phenological events (either FFD or LFD) between control and experimentally warmed plots at each site and year for every species that occurred in both treatments. Then the phenological niches of each species were compared to the difference in the number of days between the FFD or the LFD in experimentally warmed and control plots for each species, site, and year combination. Mean site-level summer temperature was not included as a predictor variable in the warming experiment analyses because the amount of experimental warming differed between experiments at different sites (Supplementary Table 3). We also examined how differences in the amount of warming in different warming experiments may have altered

results by calculating the difference in the number of days between the FFDs or the LFDs in experimentally warmed and control plots divided the mean number of degrees of warming reported for chambers at each site or subsite within site (Supplementary Table 3) to get an estimate of the change in flowering date per °C of warming.

In total, the analyses of FFDs in warming experiments included 1219 flowering observations from 164 unique site by species combinations at 16 sites. Analyses of LFDs in warming experiments included 743 observations from 96 unique site by species combinations at 11 sites.

Statistical analyses of effects of phenological niches on sensitivity of flowering

To statistically analyze phenological observations over the different numbers of sites, years of observations, and species, we used Bayesian hierarchical modeling. This approach allowed for estimation of the uncertainties of phenological responses among sites, plots, years, and species, and the incorporation of these uncertainties in the final correlation of phenological niche and phenological responses per species per site [73].

For data from long-term monitoring plots, we used two-level regression models. At the lower level, we estimated phenological sensitivities by relating the date of phenological events (FFD or LFD) to temperature or snowmelt date. At the higher (species-) level, we related species' phenological sensitivities to their phenological niches. For data from warming experiments, the difference (in days) of FFD or LFD between warmed and control plots was directly included as a response variable in the species-level regression.

We fit Bayesian models using the program Stan [74], which was accessed using the package Rstan [75] in the statistical program R 3.2.2 [76]. Each model was run with 2 chains of 20,000 iterations, using Hamiltonian Monte Carlo (HMC) sampling. We used flat priors for all parameter estimates. Full model details and code are included in S7. We checked for convergence of chains for all parameters both visually with trace plots and with the Gelman–

395 Rubin convergence statistic [77]. Trace plots showed that chains mixed well and converged to
396 stationary distributions for all parameter estimates. Gelman–Rubin convergence statistics for
397 parameter estimates of all models were < 1.02.
398
399 ***Duration of flowering season***
400 To test for a contraction of community-level flowering seasons in association with
401 warmer summers, we conducted analyses that only included sites with FFDs and LFDs for
402 four or more species over 10 or more years. This limited analyses to the six Arctic sites with
403 long-term monitoring data: Alexandra Fiord, Atqasuk, Utqiaġvik, Daring Lake, Toolik Lake,
404 and Zackenberg. Flower count or peak flowering data were not available for all sites, so we
405 used a proxy for the community flowering season calculated as the number of days between
406 the average FFD of the earliest flowering species at a site per year and the average LFD of the
407 latest flowering species at a site per year. We used the earliest and latest flowering species in
408 each year to avoid any bias caused by uneven shifts in flowering times among species.
409 Although changes in first and last flowering dates are not always representative of changes
410 over the entire flowering season [78,55], we believe our proxy can provide an estimate of how the
411 length of the flowering season may change with future warming. Additionally, a previous
412 synthesis found that reproductive phenological events within the same species are highly
413 correlated [7].
414 We compared this proxy for the duration of the community-level flowering season to
415 the average June-July temperature at a site per year using a Bayesian hierarchical modeling
416 approach. We mean-centered both flowering season length and average June-July
417 temperatures for each site so we could compare the change in community-level flowering
418 seasons with the change in June-July temperatures across sites. Because all sites chosen for
419 these analyses had relatively long records of phenological measurements (>10 years), we also
420 examined if flowering season length or June-July temperatures have changed significantly

over time. We analyzed associations between community flowering season length and summer temperature and time with a Bayesian hierarchical model using mean-centered June-July temperature as the predictor variable for the temperature sensitivity models and year as the predictor variable for the temporal change models and an intercept and slope that varied by site. We also examined whether mean June-July temperatures changed over time using the same models with year as the predictor variable. Full model details and code are included in S7.

Data Availability Statement

The data that support the findings of this study have been archived at the Polar Data Catalogue (data has been submitted to the Polar data catalogue - CCIN reference number 12961 -DOI will be updated when data is approved).

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Author contributions

J.P. and C.R. designed and led the manuscript; J.P. and C.R. led the collection of the phenology database; J.P., N.R., A.B., I.M.S. and S.E performed statistical analyses; J.P., C.R., N.R., T.H., A.B., I.M.S. and S.E drafted the paper; J.P., C.R., A.B., I.M.S., I.A., N.C, C.C., E.C., B.E., A.M.F, G.H., R.H., I.S.J., K.K., C.K., E.L., M.M., U.M., S.N., S.O., Z.P., E.P., S.R., N.M.S., E.S., P.S, J.S, K.K, Ø.T., T.T., S.V., C. W., J.W., and S.W. contributed data; and all authors were involved in writing and editing the manuscript.

Competing Interests

The authors declare no competing interests.

Figure Legends

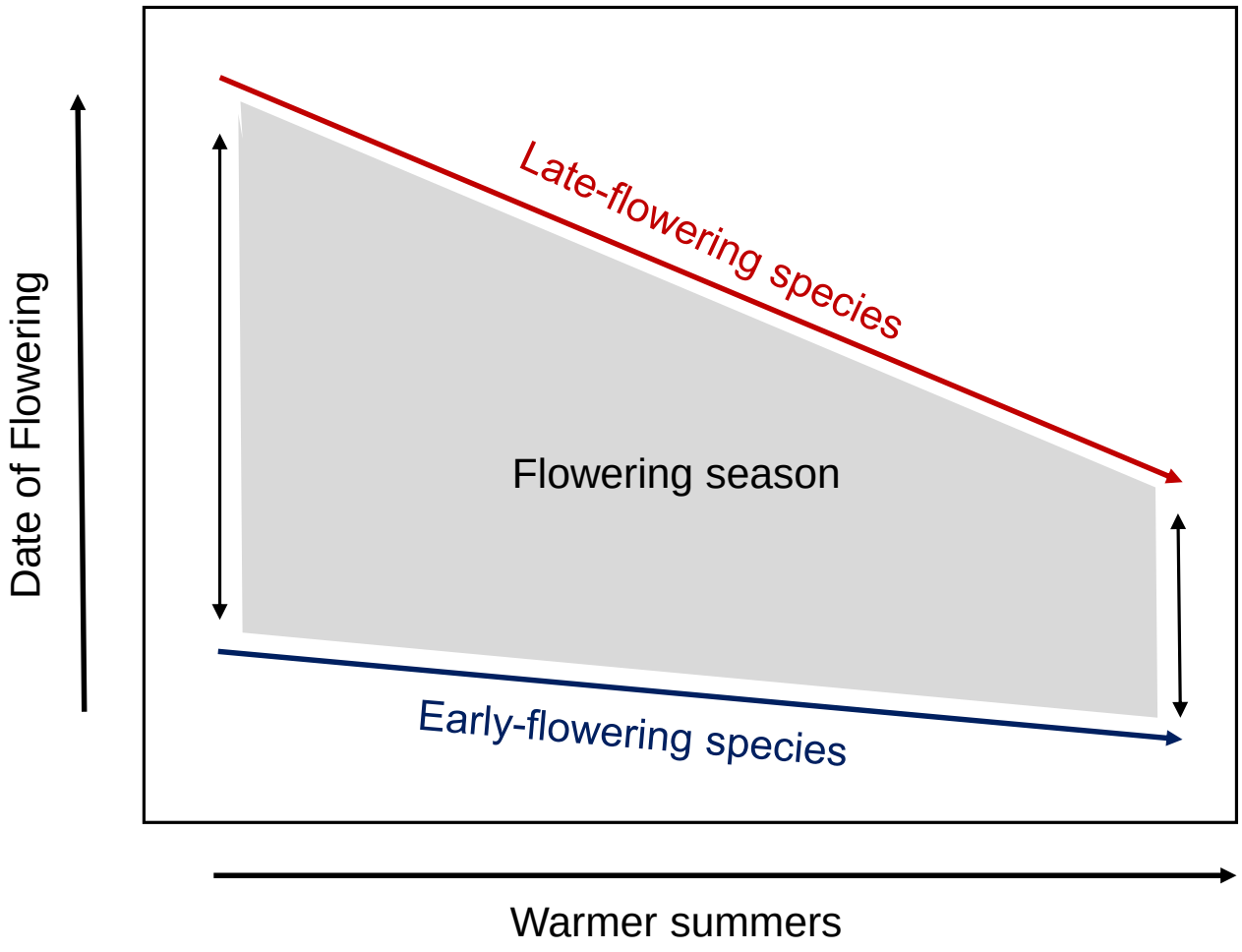
Fig. 1. Conceptual diagram showing how warmer summer temperatures may shorten the length of the flowering season in tundra ecosystems. If the phenology of early-flowering plant species is influenced primarily by photoperiod or the timing of snowmelt and does not respond appreciably to warmer summer temperatures, but the phenology of late-flowering species is mostly dependent on accumulated heat sums over the growing season, and does shift earlier with warmer summers, then there may be a contraction of the overall flowering season during warmer years.

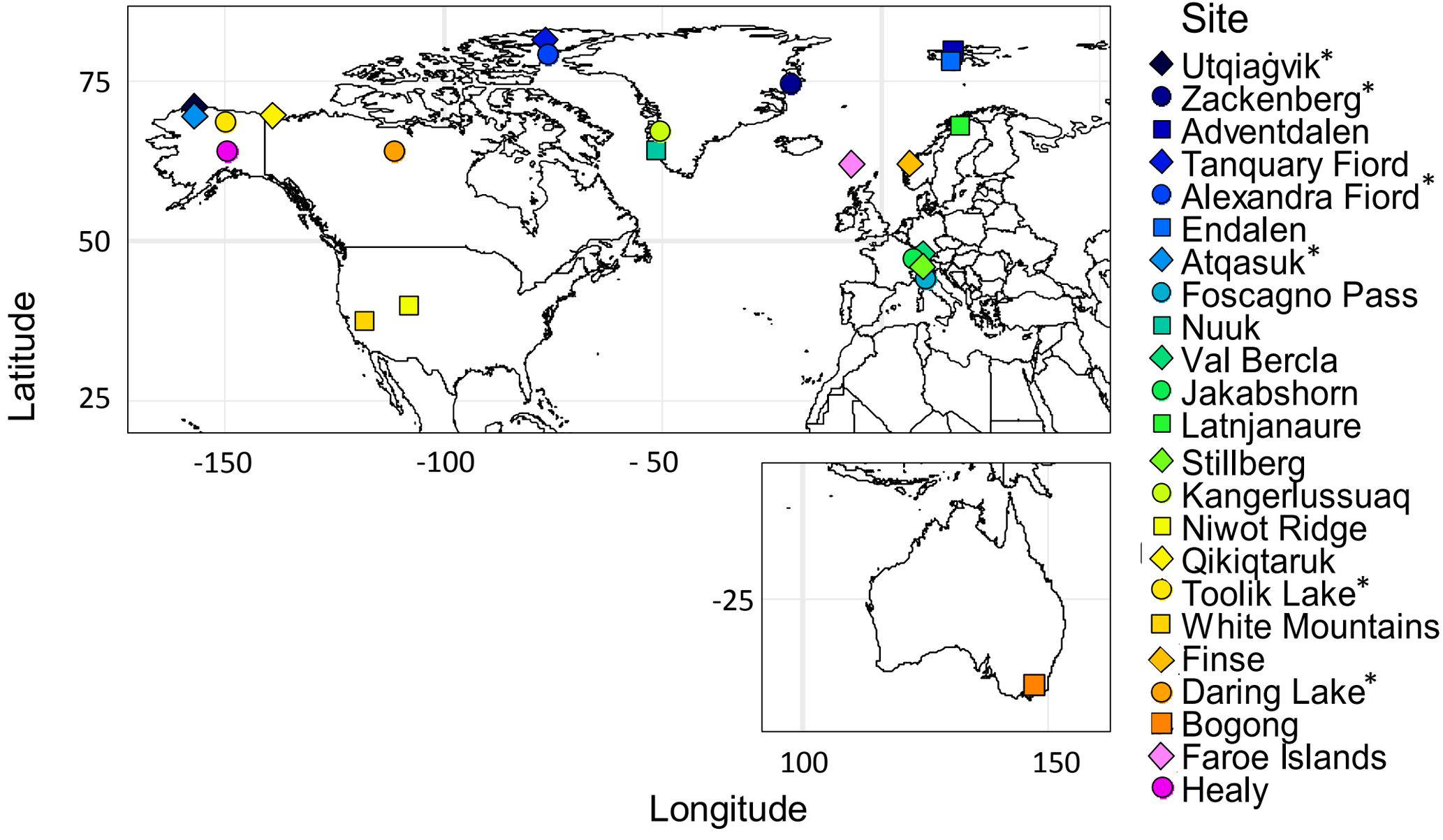
Fig. 2. Map of long-term observational and experimental warming studies. Site names are listed in order from the site with the coldest (2.8 °C) to the site with the warmest (11.9 °C) summer temperatures (June-Aug. for northern hemisphere sites, Dec-Feb. for the southern hemisphere site, Supplementary Fig. 1). Site symbols shown on the map correspond to symbols and colors in Figs. 3-4. Asterisks indicate sites used in community flowering season analyses.

Fig. 3. Temperature sensitivity of first flowering dates (FFDs) was greater for late- versus early-flowering species. Relationships are shown between phenological niches of species and sensitivities of FFDs to **(a)** mean monthly temperature until flowering **(b)** mean June temperature **(c)** mean daily temperature between the snowmelt and flowering, and **(d)** the date of snowmelt. Points represent the estimated temperature sensitivities for each species at each site, and vertical gray lines span the 95% credible intervals for each species-by-site level estimate. Colors and symbols correspond to site names in Fig. 2. The 'phenological niche' is the average flowering date of a species compared to the site-level mean-flowering date of all species at a site. Solid black lines denote significant hierarchical model slopes, dashed black lines indicate non-significant model slopes, and the horizontal grey line denotes the zero line. Hierarchical model slopes and 95% credible intervals (CIs) are listed in the bottom left of each graph. The phenological niches significantly predict phenological responses (at the 5% level) if the 95% credible intervals do not overlap zero.

Fig. 4. The change in first flowering dates (FFDs) in response to experimental warming was greater for late- versus early-flowering species. Relationships are shown between phenological niches of species and timing of **(a)** FFDs and **(b)** Last flowering dates (LFDs) in experimentally warmed plots compared to control plots. Points represent the estimated temperature sensitivities for each species at each site, and vertical gray lines span the 95% credible intervals for each species-by-site level estimate. Colors and symbols correspond to site names in Fig. 2. The 'phenological niche' is the average flowering date of a species compared to the site-level mean-flowering date of all species at a site. Solid black lines denote significant hierarchical model slopes, dashed black lines indicate non-significant model slopes, and the horizontal grey line denotes the zero line. Hierarchical model slopes and 95% credible intervals (CIs) are listed in the bottom left of each graph. The phenological niches significantly predict phenological responses (at the 5% level) if the 95% credible intervals do not overlap zero.

Fig. 5. Warming was related to the change in the duration of the flowering season over time at sites across the tundra biome. **(a)** Difference in the duration of the community level flowering season compared to the difference in mean June-July temperatures from site averages. (**b**) Change in the duration of the community level flowering season over time. **(c)** Yearly June-July temperature over time. Flowering season length and average June-July temperatures were mean-centered for each site so they could be compared across sites. Points represent the change in the community-level flowering season per site and year. Solid black lines denote significant hierarchical model slopes, and dashed black lines indicate non-significant model slopes. Colored bands show the 95% credible intervals for site-level slopes. Hierarchical model slopes and 95% credible intervals (CIs) are listed in the bottom left of each graph.


Late-flowering species
Flowering season
Early-flowering species
Date of Flowering
Warmer summers


Latitude
75
50
25
-150
-100
- 50
-25
100
150
Longitude
Site
Utqiaġvik*
Zackenberg*
Adventdalen
Tanquary Fiord
Alexandra Fiord*
Endalen
Atqasuk*
Foscagno Pass
Nuuk
Val Bercla
Jakabshorn
Latnjanaure
Stillberg
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White Mountains
Finse
Daring Lake*
Bogong
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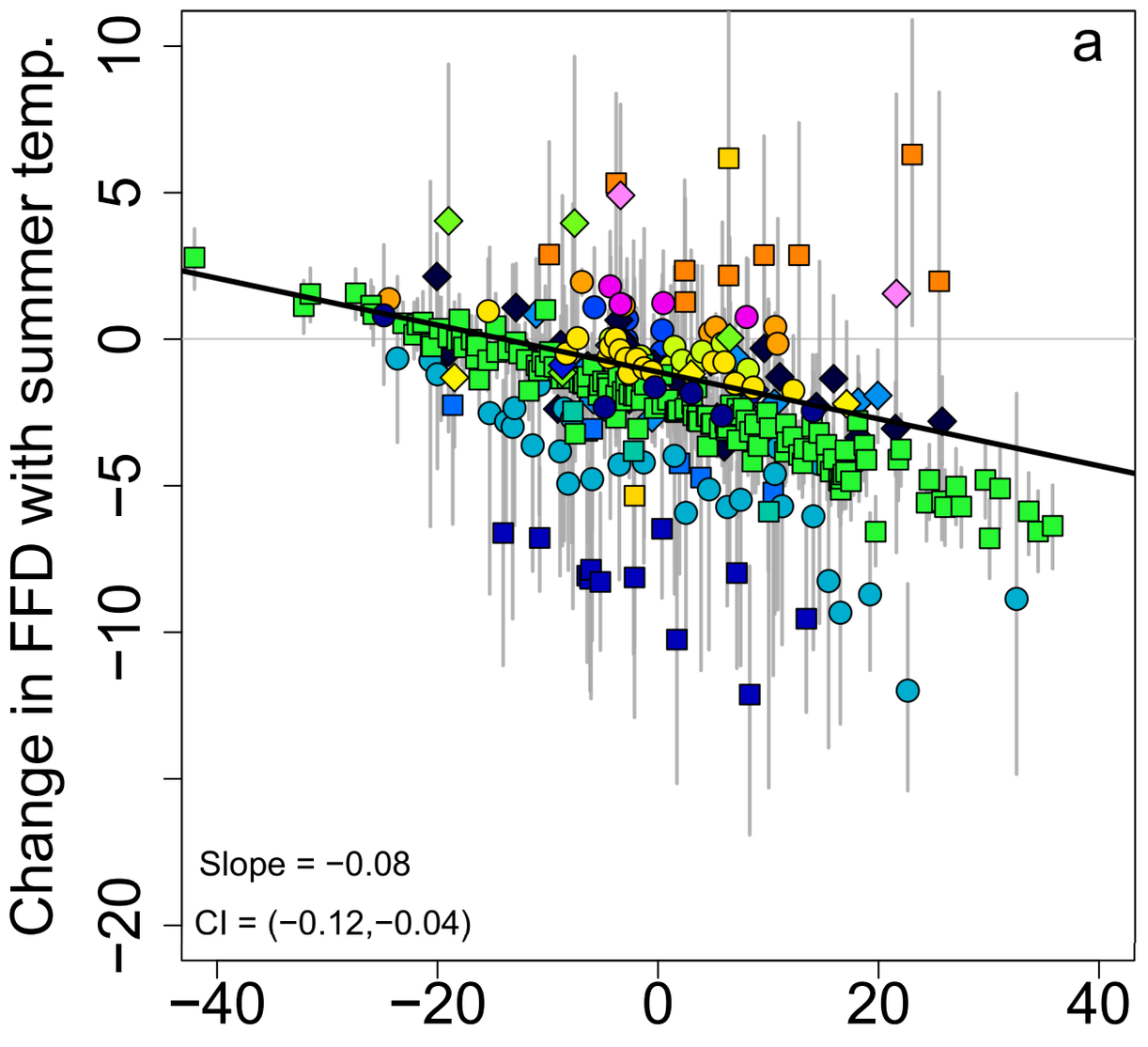
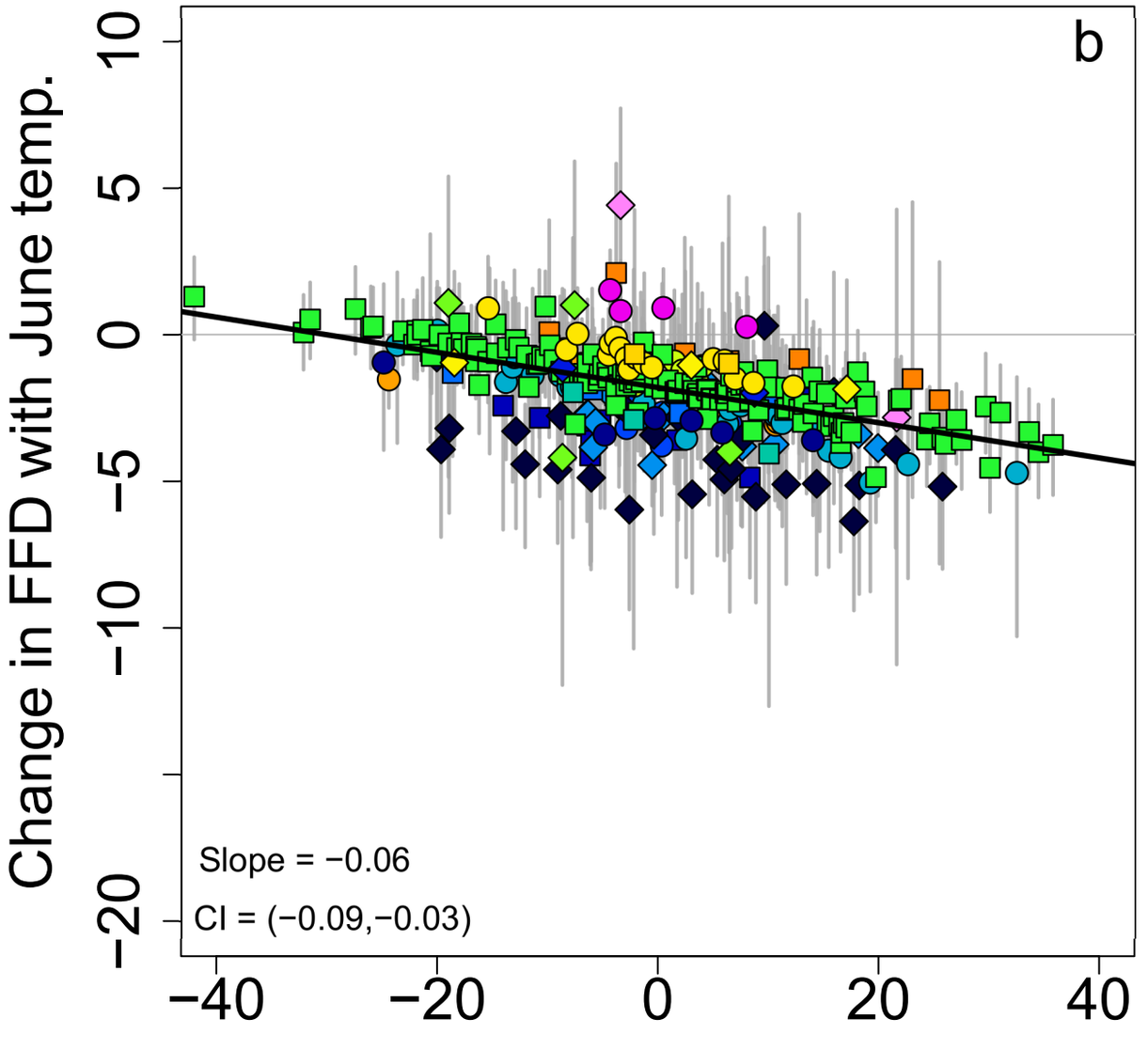
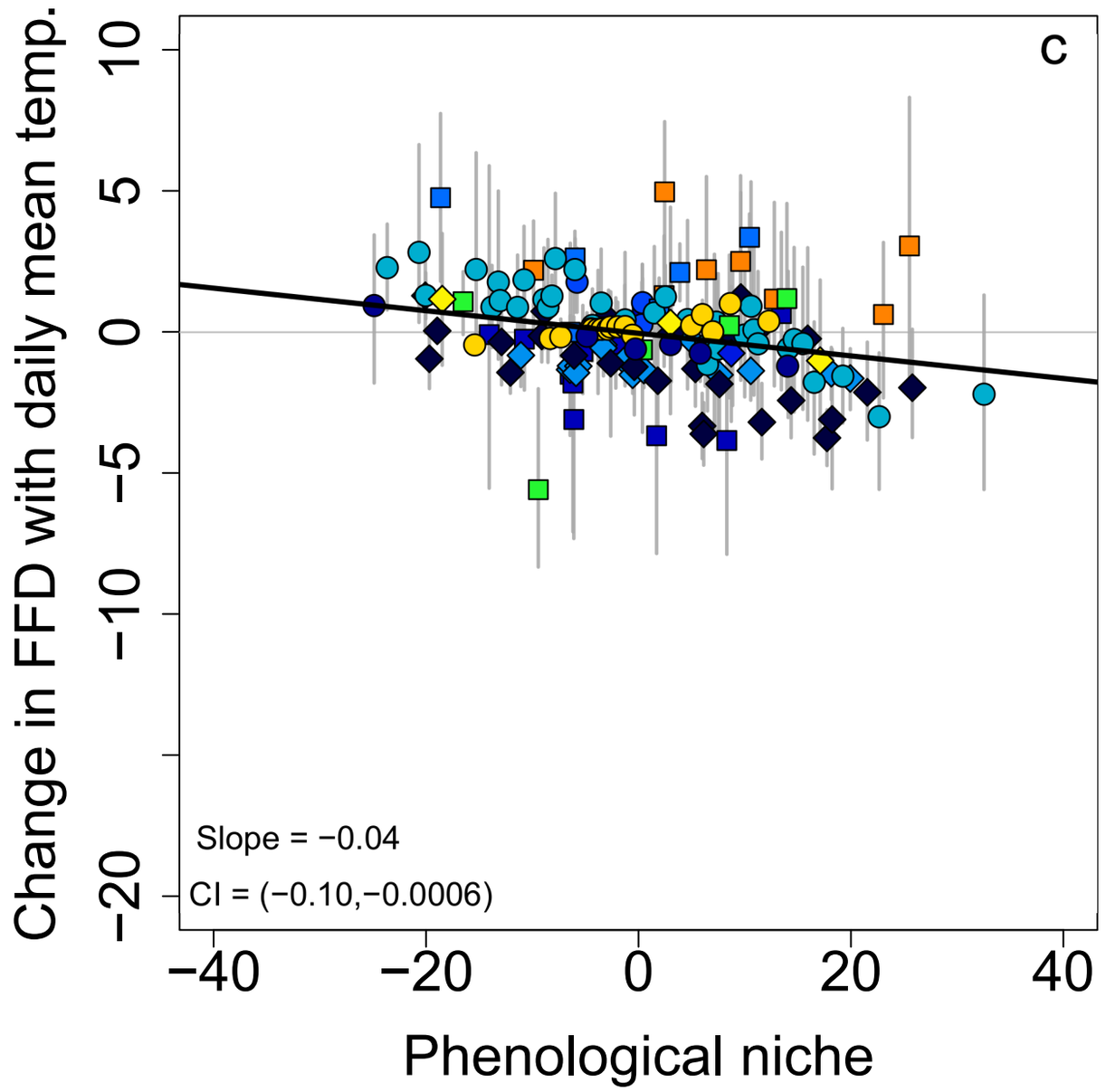
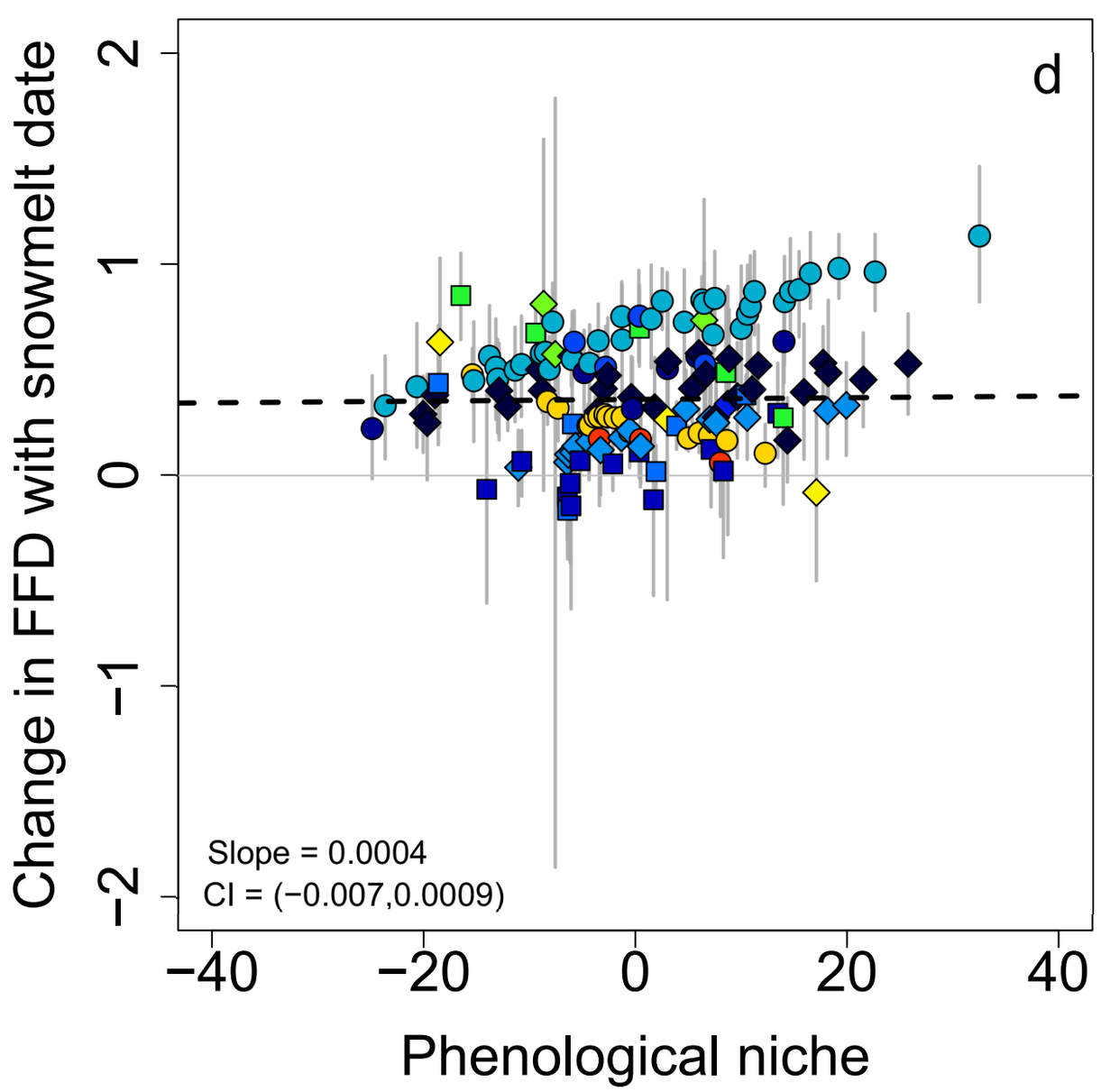
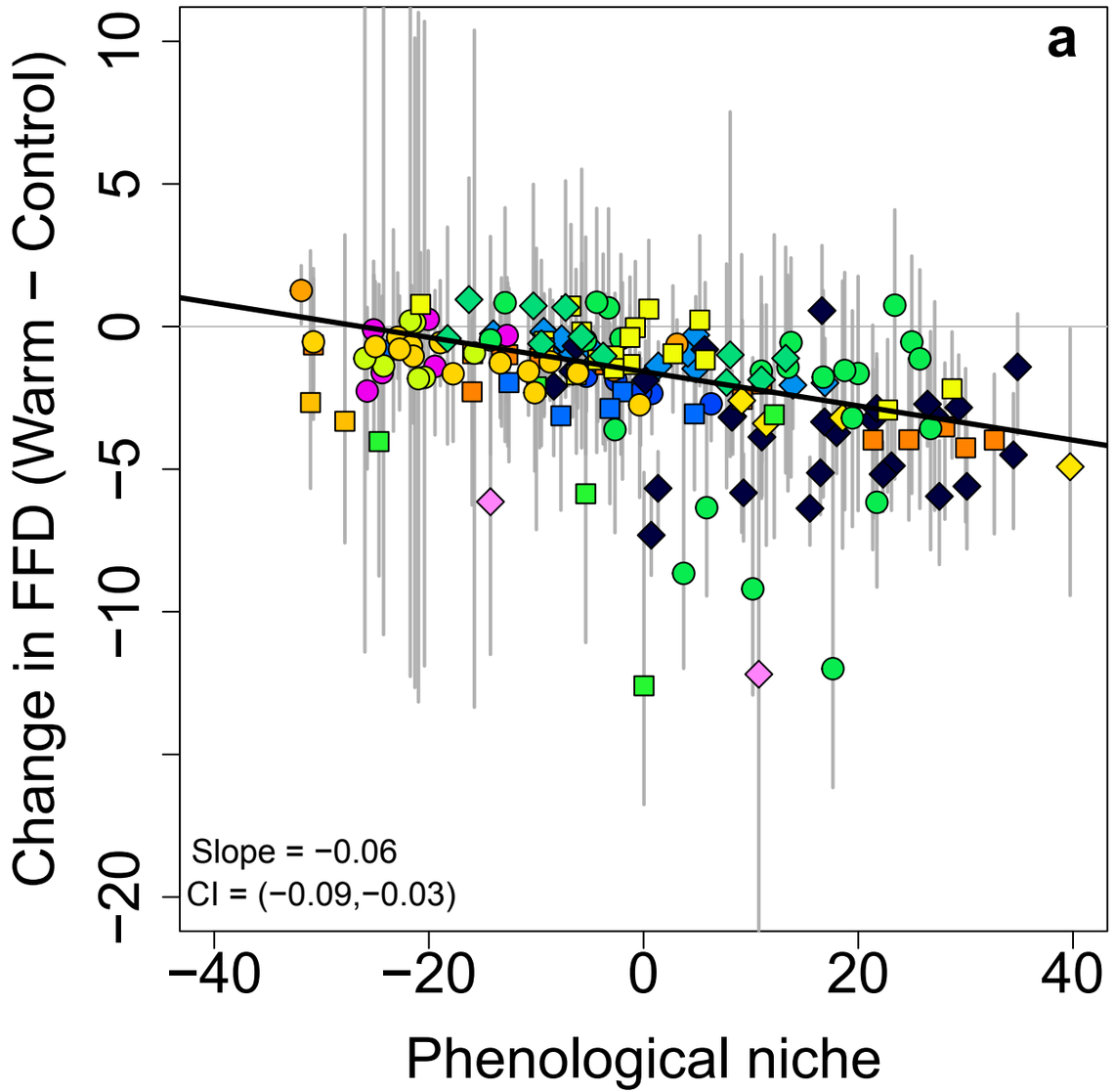
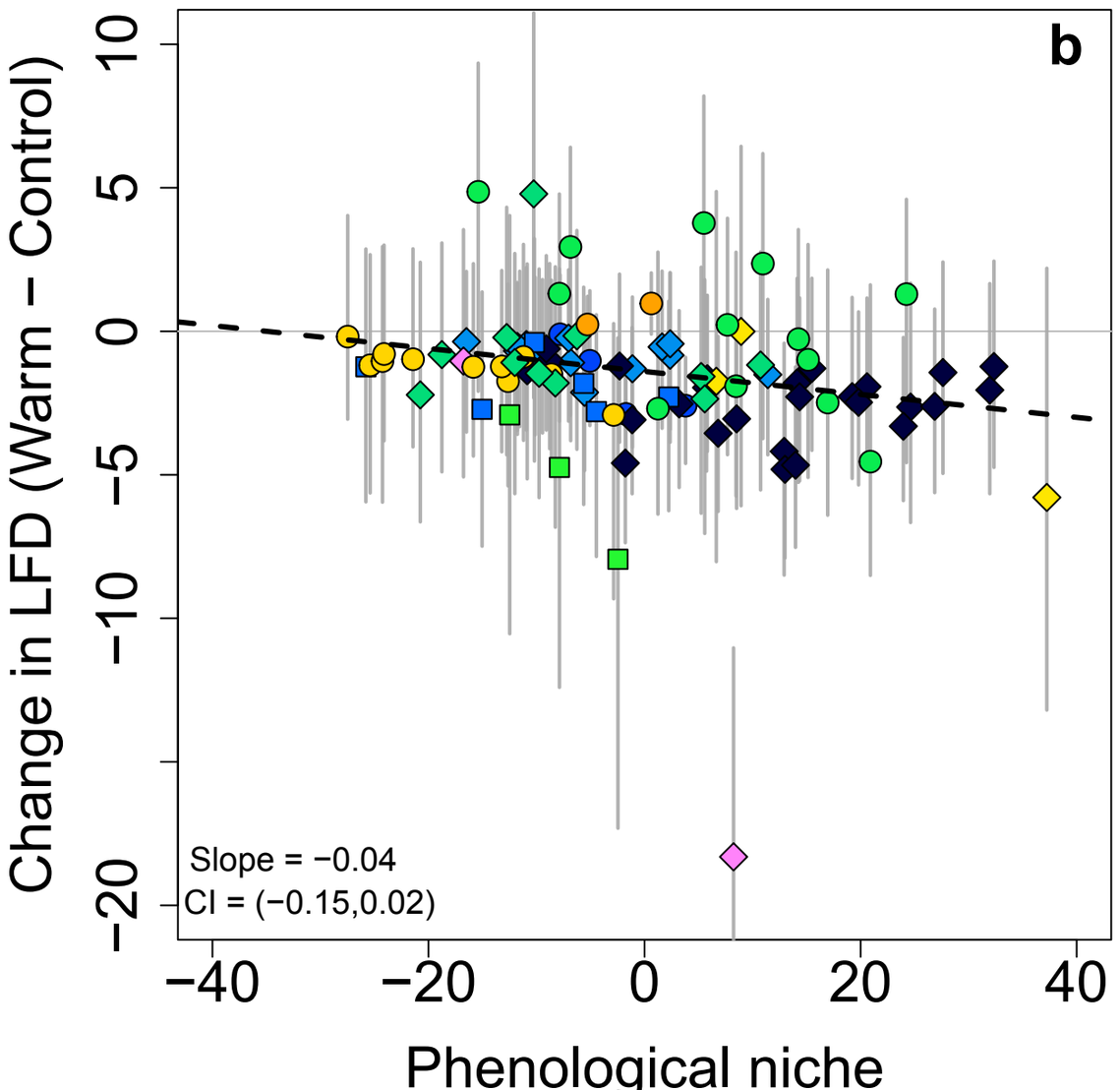

a
Change in FFD with summer temp.
Slope = −0.08
CI = (−0.12,−0.04)
10
5
0
−5
−10
−20
−40
−20
0
20
40

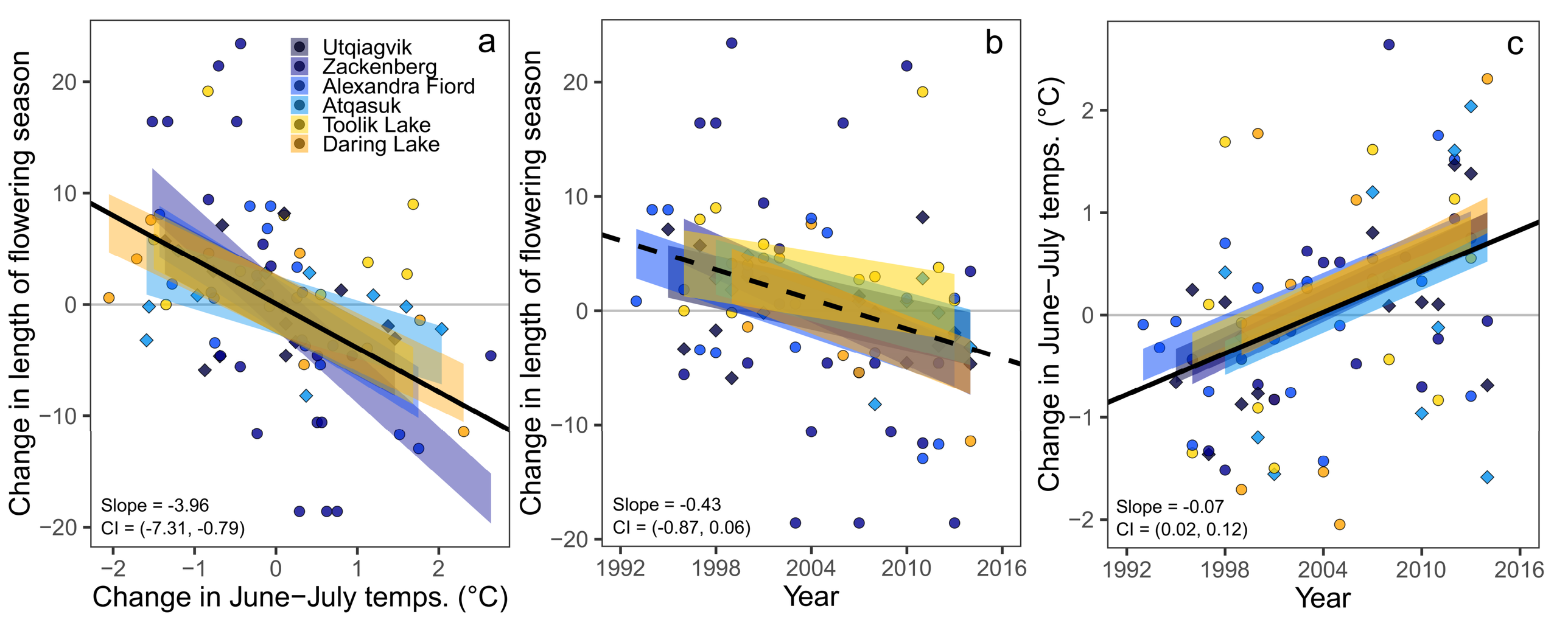

b
Change in FFD with June temp.
Slope = −0.06
CI = (−0.09,−0.03)
10
5
0
−5
−10
−20
−40
−20
0
20
40


c
Change in FFD with daily mean temp.
Slope = −0.04
CI = (−0.10,−0.0006)
10
5
0
−5
−10
−20
−40
−20
0
20
40
Phenological niche


d
Change in FFD with snowmelt date
Slope = 0.0004
CI = (−0.007,0.0009)
2
1
0
−1
−2
−40
−20
0
20
40
Phenological niche


a
Change in FFD (Warm − Control)
10
5
0
−5
−10
−20
−40
−20
0
20
40
Phenological niche
Slope = −0.06
CI = (−0.09,−0.03)


b
Change in LFD (Warm − Control)
10
5
0
−5
−10
−20
−40
−20
0
20
40
Phenological niche
Slope = −0.04
CI = (−0.15,0.02)


a
b
c
Utqiagvik
Zackenberg
Alexandra Fiord
Atqasuk
Toolik Lake
Daring Lake
Change in length of flowering season
Change in June−July temps. (°C)
Year
Slope = -3.96
CI = (-7.31, -0.79)
Slope = -0.43
CI = (-0.87, 0.06)
Slope = -0.07
CI = (0.02, 0.12)